

NEST STRUCTURE AND REPRODUCTION IN THE
MOUND-BUILDING ANT *FORMICA*
OPACIVENTRIS EMERY IN WYOMING¹

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This report records observations on mound structure, reproduction and relationships among nests of *Formica opaciventris* Emery a hitherto little-known Western species of ant. This information has relevance as a contribution to our understanding of the ecology, behavior and social structure of the *exsecta* group of the subgenus *Formica* to which *Formica opaciventris* is assigned.

Extensive observations were carried out during June, July and August of 1957 and 1959, with brief two-week visits to the mounds in 1956 and 1958. The study area is located on Moose Island, a small island, one-half by one-quarter mile in size, located in an ox-bow of the Snake River, two miles east of Jackson Lake in Teton County, Grand Teton National Park, Wyoming. The island is at an elevation of 6775 feet and is placed in the Transition Life Zone by Cary (1917).

The central portion of Moose Island, where the mounds of *F. opaciventris* are situated, consists of a silver sagebrush, *Artemisia cana*, meadow in which *Festuca idahoensis* and *Taraxacum officinale* are dominant in the understorey. The soil is a rich, black, organic loam. The meadow is bordered on four sides by the shoreline, a lodgepole pine stand, a quaking aspen stand and

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a low wet sedge meadow. Portions of the central and southern parts of the silver sagebrush meadow contain swales in which a sedge, *Carex* sp. is the dominant plant. The swales were covered with standing water during June and early July of 1956 and 1957. Approximately 400 mound nests of *Formica opaciventris* are distributed throughout most of the meadow with but few mounds along the pine forest and aspen ecotones and none in the swales.

The *exsecta* group of *Formica* in North America comprises three species; *exsectoides*, *ulkei* and *opaciventris*, and they range from the Atlantic coast through the Rocky Mountain region. There is some overlap in range between *exsectoides* and *ulkei* in Illinois and Indiana, and *exsectoides* and *opaciventris* in Colorado and New Mexico (Gregg, 1952; Cole, 1954). The distribution of *opaciventris* is poorly defined but probably includes western Montana as well as Wyoming, Colorado and New Mexico.

Formica opaciventris was described by Emery as a variety of *exsectoides*, based on his examination of workers only. Wheeler (1913) changed this status to that of a subspecies of *exsectoides* and added the description of a single male specimen. Creighton (1950) elevated *opaciventris* to specific status on the grounds that the workers are as distinct from *exsectoides* as are the workers of *ulkei*. Gregg (1952) described the female of *opaciventris* and noted that the differences between the females of *opaciventris* and *exsectoides* were not great.

Both *exsectoides* and *ulkei* are rich in striking patterns of behavior and have been studied repeatedly. Both species build large earthen mounds which they cover with thatch, these nests occurring as large aggregations of mounds. McCook (1877) estimated that a population near Hollidaysburg, Penna., included 1700 *exsectoides* mounds, and in Illinois Dreyer and Park (1932) counted more than 450 *ulkei* mounds. Both species are polygynous and exhibit secondary pleometrosis in which mated females return to established nests (Wheeler, 1906; Cory and Haviland, 1938; Scherba, 1958). New mounds are formed by budding from established nests and by temporary social parasitism of *Formica fusca* Creighton, 1934, 1950). In the European species *Formica exsecta*, single colonies are reported to occupy more than 100 nests interconnected by runways, so-called polydomous or polycalic colonies (Forel, 1928). While this has not been reported

for the North American species, *Formica exsectoides* workers "visit" between nearby mounds (Wheeler, 1928).

It is of considerable interest to determine which of these traits is present in *F. opaciventris*, and the extent to which differences exist among the species in this group of closely related ants.

NEST STRUCTURE

The nests of *Formica opaciventris* at Moose Island are low, conical earthen mounds, varying in size up to a basal diameter of 78 inches and a maximum height of 24 inches at the mound apex. These mounds are asymmetrical and have a long, broad slope oriented toward the east, southeast, or rarely, south. A census of the slope direction of 95 active mounds with a clearly discernible long slope indicated 52 mounds sloping to the east; 42 sloping to the southeast, and one mound partially shaded on the east, sloping to the south. Presumably the long slope face indicates that direction in which optimal conditions for nest construction are present for the longest periods of time.

The mound crust of consolidated, compact soil is overlain by a thin layer of freshly mined soil particles. Scattered lightly and irregularly over this is a covering of thatch, consisting of plant debris; leaf petioles, dead grass stems, pine needles, occasional green tips of rush, seed coats and the like. The lower slopes and basal areas of the mounds are fringed by a growth of rush, *Juncus* sp. probably *Juncus balticus*, whose underground stems, roots and rhizomes are thickly entangled, buttressing the mound structure. While the apex and upper slopes of the most populous and active mounds are bare of vegetation, *Juncus* is thinly scattered over the upper surfaces of the less vigorous mounds, growing highest on the west facing slopes. Extending horizontally outward from the basal surface of active mounds for up to 15 inches is an apron of mined soil with numerous nest entrances. Scattered nest entrances also occur from the base to the apex on all slopes.

On August 12, 1959, nest 459, a medium sized active mound was excavated to a depth of five feet below the level of the soil surface. The following description of the mound structure is based on this nest.

The mound interior consists of soil together with a small amount of undecomposed vegetative debris. Horizontal circular

and vertical galleries varying in diameter up to one-half inch honeycomb the mound portion of the nest except at the basal margin, the area of dense *Juncus* roots. Galleries within the mound itself are numerous but their density decreases in the soil beneath the mound. There is a striking coincidence between the decrease in gallery density and the soil profile. In the mound and upper loamy soil layer, galleries are numerous down to a depth of approximately 8 inches beneath the soil surface. In the B horizon the soil becomes blocky and enriched with clay. Here the galleries are less dense although abundant down to a depth of two feet below the soil surface. In the C horizon, beginning at about two feet below the soil surface, the soil is hard, contains silt and very fine sand and is structured as large angular blocks. A few scattered galleries are present here and some of these extend vertically to a depth greater than five feet below the soil surface.

In the mound examined, and possibly unique to that mound, was a large oval chamber, six inches in length, 4 inches in height and approximately four inches deep. This chamber was situated eight inches below the mound apex at the level of the adjacent soil surface. The chamber was filled with undecomposed thatch and fine bits of organic debris of a size that could have been carried into the nest by the workers. The function of this cavity was not apparent, and a corresponding cavity could not be found in two similar mounds which were examined. Our present interpretation is that the chamber originated as a damaged or trampled portion of the mound which was filled with thatch and covered over with soil particles.

THATCHING BEHAVIOR In an attempt to determine some of the factors effecting nest-building behavior, field experiments were conducted on the effect of moisture on the rate of thatching. Moisture was chosen because of repeated observations recorded in the literature, that nest building activity increases following rainfall (e.g. Wesmann, 1905). Recent experiments on other aspects of nest building have been conducted by Chauvin (1958, 1959a, 1959b).

In each of three experiments two areas each of 16 square inches of nest surface were delineated and the number of pieces of thatch carried into these areas by the workers was counted and removed each day. The experimental area and the entire

mound slope containing it was sprinkled with 5 litres of water from a sprinkling can each day. The control area and the slope containing it was not watered.

In Experiment 1, the rate of thatching by workers of nest **317**, watered, was contrasted with that of adjacent, similar, nest **316**, unwatered. After three days the watering schedule was reversed and nest **316** was watered.

In Experiment 2, the east facing slope of nest **323**, watered, was contrasted with the unwatered west facing slope. After 4 days the watering schedule was reversed.

In Experiment 3, the northeast slope of nest **198**, watered, was contrasted with the unwatered southeast slope.

Results are arranged as Table I. The data indicate that the effect of watering is to increase the rate of thatching, hence watered slopes are thatched to a greater extent than unwatered slopes. Reversal of the watering schedule resulted in a reversal of the relative thatching rates, indicating that the observed results are due to effects of watering and not to other differences existing between the experimental and control areas. The data have been further examined using a t-test for paired comparisons and the amount of thatch carried onto watered slopes is significantly greater than that carried onto unwatered slopes ($t = 11.2$; $p < .01$). There is considerable day-to-day variation in thatching rate on both watered and unwatered slopes. This may reflect the effect of other environmental factors, such as temperature, on thatching rate.

REPRODUCTION

Formica opaciventris resembles the other North American *exsecta* species in maintaining polygynous colonies. A small nest, **290**, excavated on June 26, 27, 1957, contained 101 active dealate females.

Males occur in two distinct size classes. Total length measurements of 23 males from several mounds indicates a *micraner*, 6.5–8 mm. and a *macraner*, 9.0–10.1 mm. using the terminology of Wheeler (1910). The *micraner* appear smaller and more slender but otherwise are similar to the *macraner*. Both sizes have been observed in the same colony, although some mounds contain only one class. Both sizes have been observed to copulate with *opaciventris* females, and no functional differences are apparent.

TABLE I

NUMBER OF THATCH PARTICLES BROUGHT BY WORKERS ONTO
WATERED AND UNWATERED NEST SLOPES

Experiment 1

Numbers bearing asterisk are tallies made on watered nests

Date	Nest 316	Nest 317
August 6, 1959	97	88
7	55	87*
8	62	127*
10	85	134*
11	210*	130
12	243*	122
13	247*	177
14	227*	106
15	243*	100
16	276*	75

Experiment 2—Nest 323

Numbers bearing asterisk are tallies made on watered slopes

Date	East Slope	West Slope
August 6, 1959	40	62
7	81*	27
8	121*	32
10	86*	35
11	100*	78
12	14	72*
13	177	213*
14	22	123*
15	75	149*
16	49	160*

Experiment 3—Nest 198

Numbers bearing asterisk are tallies made on watered slope

Date	Southeast Slope	Northeast Slope
August 12, 1959	14	72*
13	177	213*
14	22	123*
15	75	149*
16	49	160*

SEASONAL LIFE CYCLE Eggs are present in the mounds in June and they complete development to adult worker or sexual in August, a pattern similar to that observed in *F. ulkei*. Mating flights occur in August with new nests formed by budding. Nest 153, believed to be formed by budding during June or July, 1957, was excavated on July 25 of that year. The population consisted of approximately 30 workers without brood or sexuals.

PRODUCTION OF SEXUALS In the course of observations on mating behavior in 1957 it appeared that not all mounds were releasing sexuals and that among the mounds in which sexuals were produced, some released only males, some only females, others both males and females. Systematic observations were then attempted to determine the percentage of mounds liberating sexuals, here called fertile mounds, and to determine the proportion of male releasing to female releasing mounds.

TABLE II
NUMBER OF WINGED SEXUALS OBSERVED ON MOUND SURFACE
BEFORE MATING FLIGHTS, 1957

Date	Nests Inspected	Males	Females
Aug. 12	25	1	3
14	45	135	8
15	108	1355	65
16	88	3	6
TOTAL	152	1494	82
RATIO		18.2	: 1

In 1957, 152 mounds were censused between August 12 and 16 during the early morning interval between the time that the sexuals emerge from within the nest to parade over the mound surface, and flights begin. The number and caste of winged adults was estimated for as many mounds as could be visited each day. As a result of the information gathered in 1957 the census was repeated between August 15 and September 1, 1959, omitting the estimate of the number of sexuals per nest in order to examine a greater number of mounds. It should be clear that the number of sexuals recorded as observed on the mound surface in 1957 (Table II) represents a best estimate of the actual number present. A precise count is not easily obtained under such circum-

stances. Further, mounds are tallied as fertile or sterile on the basis of the presence of winged sexuals on the mound surface at the time of census without excavation of the mounds at any time.

TABLE III

PROPORTION OF MOUNDS ON WHICH SEXUALS WERE OBSERVED EACH DAY
DURING MATING PERIOD. AUGUST 1957 AND 1959

Date	Mounds Inspected	Only ♂	%	Only ♀	%	Both ♂ and ♀	%
Aug. 12, 1957	25	1	4.0	2	8.0	0	0
14	45	11	24.4	0	0	2	4.4
15	108	25	23.1	0	0	7	6.5
16	45	3	6.7	1	2.2	0	0
Aug. 15, 1959	137	22	16.1	2	1.5	1	0.7
16	144	20	13.9	1	0.7	2	1.4
17	210	39	18.6	2	0.9	1	0.5
18	239	25	10.5	3	1.3	2	0.8
23	145	17	11.7	3	2.1	3	2.1
24	252	24	9.5	2	0.8	4	1.6
28	218	10	4.6	3	1.4	2	0.9
Sept. 1	205	0	0	1	0.5	0	0

Date	Total ♂	%	Total ♀	%	Total Mounds With Sexuals	%
Aug. 12, 1957	1	4.0	2	8.0	3	12.0
14	13	28.9	2	4.4	13	28.9
15	32	29.6	7	6.5	32	29.6
16	3	6.7	1	2.2	4	8.9
Aug. 15, 1959	23	16.8	3	2.2	25	18.3
16	22	15.3	3	2.1	23	16.0
17	40	19.0	3	1.4	42	20.0
18	27	11.3	5	2.1	30	12.6
23	20	13.8	6	4.1	23	15.9
24	28	11.1	6	2.4	30	11.9
28	12	5.5	5	2.3	15	6.9
Sept. 1	0	0	1	0.5	1	0.5

The release of sexuals extended over a period of several days both in 1957 and 1959. During the period of mating flights in 1957 the number of sexuals observed on the mound surface increased abruptly to a maximum on August 15 and then declined sharply. Males and females were observed in a ratio of approximately 18 : 1 (Table II). The number of sexuals observed on the

mound surface varied widely from mound to mound. Some nests released as many as 300 males while the number of females observed at a single mound did not exceed 41.

Not all of the mounds examined in 1957 and 1959 were fertile. Instead, a reproductive division of labor existed with fertile nests comprising between 20% and 25% of the population. The proportion of fertile nests observed on any individual day varied from 7% to 30% of the nests sampled that day, with a decrease in the proportion of fertile mounds occurring abruptly in 1957 and gradually in 1959, at the end of the flight season (Table III).

Nests liberating males were more numerous than those liberating females with a male : female ratio of 5.5 : 1 in 1957, and 7.6 : 1 in 1959. Most of the nests which produced females also produced males, with a ratio of male only : female only mounds of 30 : 1. Nests releasing both males and females comprised be-

TABLE IV

OVERALL PROPORTION OF MOUNDS ON WHICH SEXUALS WERE OBSERVED
AUGUST 12-16, 1957 AND AUGUST 15-SEPTEMBER 1, 1959

	1957		1959	
	Number	%	Number	%
Mounds Censused	152		326	
Sterile	115	75.7	256	78.5
Fertile	37	24.3	70	21.5
♂ Only	29	19.1	61	18.7
♀ Only	1	0.7	2	0.6
♂ and ♀	7	4.6	7	2.1
Ratio of male : female releasing mounds	5.5 : 1		7.6 : 1	

tween 2% and 5% of the populations of mounds, while mounds releasing females only comprised less than 1% (Table IV). No consistent differences have been found as to appearance of the mound or the activity of the inhabitants between male producing, female producing and sterile mounds.

Of the 326 nests censused in 1959, 147 were also examined in 1957. What changes in reproductive status occurred to this population of mounds? Most of the population, 76.9%, had not changed. However, 12.2%, fertile in 1957, had become sterile by 1959 and 8.8%, sterile in 1957, had become fertile. Of the

37 mounds which were fertile in 1957, only 16, 43.2%, were still fertile in 1959. Almost 50% of these fertile nests had become sterile. Of the 8 mounds containing females in 1957, none contained females in 1959. Three mounds changed sexual status between 1957 and 1959; two from male and female producing to male only and one from male only to female and male producing (Table V).

If we assume that the proportion of mounds which become sterile or fertile each year is approximately equal and constant from year to year, then we may tentatively infer that mounds are fertile for approximately four years with 25% of the fertile population becoming sterile each year.

TABLE V
REPRODUCTIVE STATUS OF MOUNDS CENSUSED BOTH IN 1957 AND 1959

	Number	%
Nests censused	147	
Fertility status unchanged	113	76.9
Fertility changed	34	23.1
became sterile	18	12.2
became fertile	13	8.8
changed sex	3	2.0
Mounds fertile in 1957	37	
still fertile in 1959	16	43.2
sterile in 1959	18	48.6
fertile but changed sex	3	8.1

FLIGHT ACTIVITIES Observations on mating behavior in *Formica opaciventris* were conducted on August 10, 12, 15, 16, 1957, and on August 15, 17, 18, 23, 24, 1959, at the study area. Flight activities occur in the morning, between 7 A.M. and 10 A.M. and follow the sequence; emergence of the males, emergence of the females, flight of the males, flight of the females, mating, and return of the females to the mound.

The males emerge from the nest after the workers are already on the mound slopes, between 6:55 A.M. and 7:25 A.M., and they crawl aimlessly over the mound surface and cluster at nest entrances. The females emerge and also crawl over the mound surface, slowly at first, later more rapidly. Males and females parading over the mound surface occasionally meet but there is

no avoidance nor attraction apparent at this time. When workers encounter sexuals they attempt to seize them by a leg or antennae. Sexuals so caught struggle and escape.

As air temperature rises the males leave the mound surface and climb the stems of herbaceous plants growing from the mound or at the mound periphery. They climb to the tips, turn around and around, flutter their wings and continue in this manner for several minutes. The male flight begins with a final flutter, and the males depart, singly, flying low, just above the tops of the herbaceous plants.

The females parading over the mound surface now travel down the slope and into the vegetation adjacent to the mound margin, or onto stems of plants emerging from the mound. They climb to the top of the plant stem, flutter their wings and fly—usually less than ten feet, and frequently simply to a nearby plant stem three or four feet away. Some females crawl down from the plant tip and onto a second, usually higher plant, before flying. Others climb down and reënter the nest without flying. At the end of the flight season in 1959 a few females were observed to fly longer distances; 30 feet, 100 feet, 150 feet and a few flew up and away out of sight, flying strongly in the direction of increased light. These latter females originated from a nest at the eastern edge of the population of mounds, and their flight took place at a time when no males were seen.

As the males fly into the vicinity of a female-releasing nest, the females remain scattered at heights up to three feet in the vegetation at the mound periphery. The observer at the mound receives the impression that the males are not flying at random but are oriented in the direction of the few mounds at which females are released. Males fly directly to within four to six inches of a female, alight, then search about randomly in an agitated manner. When a male encounters a female, copulation occurs after brief "chasing." Copulation lasts from 40 seconds to 2 minutes and is terminated by the female who bites the abdomen of the male and pinches it with her legs, forcibly separating herself. Some females have been observed to mate twice, with a different male at each occasion.

After copulation the males fly away or flutter weakly to the surface of the ground. Foraging workers seize these males and carry them into nest openings, presumably as food. After groom-

ing, the post-copulatory females climb down the plant stem, crawl along the ground surface and re-enter the mound through an opening at the basal edge. Of three females marked with nail polish after copulation, two were lost from sight, and one was carried within the mound, intact, by workers, a pattern referred to as "escorting" in the literature. However, at another mound two post-copulatory females individually met workers near the mound and these workers made no attempt to seize or restrain them. The females re-entered the mound unescorted.

On mornings after the flight season has ended, alate females parade on the mound surface, but re-enter the mound without flying.

Recently Kanno (1959) and Talbot (1959) have demonstrated that flight activities are regulated by climatic events in several ant species, and this appears likely in *F. opaciventris* also. The morning of August 19, 1959, was cool, wet and foggy and no alates flew although flights occurred before and after that date. Male flight was interrupted on August 15, 1957, as the sky was overcast. When the sky cleared and temperatures rose, flights resumed. Air temperature measurements at a height of 12 inches indicate that when males first appear on the nest surface air temperatures are between 6.5° C. and 14.5° C.; when females first appear air temperatures are between 10.0° C. and 16.9° C. Both males and females have been observed to fly at a time that air temperatures were between 12.2° C. and 21.2° C. When mating occurs temperatures are between 13.0° C. and 21.2° C.

RELATIONSHIPS AMONG NESTS²

In August, 1959, marking experiments were conducted in order to determine whether workers at one mound also frequented other mounds. In each of four trials several hundred workers were individually taken from the surface of a mound, marked with one of 3 colors of nail polish, and replaced. Nearby mounds were later inspected for the presence of marked ants. Marking in this fashion did not appear to alter the behavior of the workers, who were later observed transporting pupae and nest building. A single marking persists for several days.

² The observations described in this section were begun in response to a suggestion of Dr. Mary Talbot, Lindenwood College, that several mound nests of *F. ulkei* may be interrelated by virtue of workers moving back and forth between mounds.

TRIAL 1 Two mounds, **468** and **470**, located contiguously with their basal edges connected by mined soil tunneled with entrances. Workers marked at **468** were found on **470**; one worker marked at **470** was found on **468**.

TRIAL 2 Three mounds, **74**, **75** and **76** arranged in a triangular manner with 9, 10 and 12 inches between the basal edges. Workers marked at **74** were found at **75** and **76**. Workers marked at **75** were found at **74** and **76**. Workers at **76** were not marked. Workers marked at both **74** and **75** were observed to carry soil as in nest building at **76**.

TRIAL 3. Two mounds, **281** and **954**, located 8 feet, 8 inches apart. **954** is believed to be a bud of **281**, founded in 1957. Workers marked at **954** were observed at **281** and workers marked at **281** were observed on **954**.

TRIAL 4 Three mounds, **206**, **321** and **294**, situated such that **206** is 3 feet, 2 inches from **321** and 15 feet from **294**. **294** is 13 feet, 5 inches from **321**, arranged in this order:

206

321

294

Workers marked at each of these nests were found on the surfaces of the other two mounds. Marked workers from each of these nests were also found on other nearby mounds. Two of these mounds were at a distance of 25 feet from **294** and one mound, **198**, with a single worker each from **206** and **294** was 55 feet from **206**. In several instances workers marked at one nest were carrying soil or empty pupal cases at another nest.

We may conclude that workers move from one mound to another up to a distance of 55 feet. The meaning and extent of these movements are unknown.

DISCUSSION

The life history of an individual mound probably follows this cycle: Mounds are formed by budding from parental nests and, in time, increase in size and in number of inhabitants. After an unknown period the condition of the population of the mound becomes such that sexuals are produced, and this reproductive period is estimated to last four years. After a further length of time the population declines, the mound becomes overgrown with vegetation and either dies or becomes rejuvenated by a reinvasion from a budding population.

Although workers evidently move back and forth between mounds, we would still consider all except incipient mounds to be separate colonies, a view already expressed by Wheeler (1928). Forel's concept of a polycalic colony, in which one colony occupies several mounds, does not appear useful in this situation. However, it is entirely possible that these colonies share a common worker pool, to the extent that, in time of need at one colony, the potential worker force available would be considerably greater than the population of workers at that mound. The adaptive value of such a system would be enormous.

The reproductive division of labor, such that only 25% of the mounds are fertile during a single season appears to be an adaptive mechanism which increases the efficiency of the population of mounds as a whole. However such a system with its exceedingly low rate of production of females can only be of selective advantage if fertilized females are afforded a maximum of protection from predators and other circumstances which might limit their survival. The abbreviated flight of the females, with return to the nest and the formation of new mounds by budding provides this maximum protection, while permitting mating of sexuals from different mounds.

Under such a reproductive pattern the unit of natural selection becomes not the individual alate, nor the individual colony, but the population of colonies. The interrelationships between mounds and the division of reproductive labor within the population are essentially integrating mechanisms which operate here at the level of the population of societies.

Is it possible to begin a tentative comparison of certain behavior traits found within the *exsecta* group in North America?

Differences in mound structure exist. While mounds of *exsectoides* and *ulkei* could not be distinguished from one another in Illinois, mounds of *opaciventris* in Wyoming have a thinner crustal layer, incorporate less vegetation, and are covered with a sparser layer of thatch. The mound slopes of *exsectoides* and *ulkei* are free of vegetation, unlike those of *opaciventris*. These differences could, of course, be due entirely to differences in environment.

The reproductive pattern appears quite similar among the three species and is consistent with the general pattern in many ant species detailed in the recent fine study of Kanno (1959).

New mounds are formed by budding in all three species, although details of this pattern are obscure and could reveal differences. Both *exsectoides* and *ulkei* form occasional mixed colonies with other species, especially *Formica fusca*, presumably by temporary social parasitism. Mixed colonies of *opaciventris* have not yet been found, although numerous *Formica fusca* colonies encircle the *opaciventris* mounds at the study area.

TABLE VI

COMPARISON OF REPRODUCTIVE BEHAVIOR PATTERNS AMONG SPECIES
IN THE *exsecta* GROUP OF *Formica*

Trait	<i>exsectoides</i>	<i>ulkei</i>	<i>opaciventris</i>
Mating flights begin	"at the close of June" (McCook, 1877)	June 26	August 15
Flight time		Early morning	Early morning
Males first appear on nests		Approx. 11.0°C.	6.5°C.-14.5°C.
Temperature at which flights occur		15°C.-22°C.	12.2°C.-21.2°C.
Mating flight of female		Strong, definite upward flight	Flight of a few feet
Behavior of mated females	Return to estab- lished nests (Wheeler, 1906)	Return to estab- lished nests	Return to nest of origin
Formation of new nests	Temporary social parasitism and budding (Creighton, 1950)	Temporary social parasitism and budding (Creighton, 1934)	Budding

The flight dates are concurrent for *exsectoides* and *ulkei* and occur approximately six weeks earlier than that of *opaciventris*. The flights of both *ulkei* and *opaciventris*, occur in the early morning hours over a period of several days. Both the temperature at which males first appear on the nest and flight temperatures are lower in *opaciventris* than in *ulkei*. Whereas in *ulkei* the flight of the females is strong, definite and upward, that of *opaciventris* is notably brief and limited, with the exception noted earlier. In all three species the mated females return to established nests, although there is no evidence that in *exsectoides* or *ulkei* females return to the mounds of their origin. In all three species workers "escort" mated females back into the nest, and

ulkei workers dealate the females on the mound surface before they enter the nest. These comparisons are summarized as Table VI, from data presented in Scherba (1958) and Talbot (1959).

SUMMARY

Field observations of a population of nests of the mound-building ant *Formica opaciventris* were conducted in 1957 and 1959 in western Wyoming.

The mound nests are galleried earthen structures covered by a layer of thatch. Thatching behavior is affected by environmental factors such that watering a portion of a mound, or an entire mound significantly increases the rate of thatching.

The mounds are polygynous, release males of two distinct sizes and form new mounds by budding. Brood development is initiated and completed within a single season.

There is a division of reproductive function among the population of mounds such that between 20% and 25% of the mounds are fertile (release alates) during each season, with a ratio of male releasing : female releasing mounds of between 5 : 1 and 8 : 1. Females are released from 3% to 5% of the mounds. It is estimated that mounds are fertile for approximately four seasons, with 25% of the fertile mounds becoming sterile each year.

Mating flights occur over a period of several days in August during the morning hours only. Mating occurs on the stems of herbaceous plants with mated females returning to the mound of their origin after a mating flight of only a few feet. This reproductive pattern differs somewhat from that of other members of the *exsecta* group, and these differences are tabulated.

Marking experiments indicate that workers at one mound can also be found at other mounds in the vicinity with a maximum observed visiting radius of 55 feet.

The reproductive division of labor and the interrelationship between workers of different mounds are interpreted as integrating mechanisms which operate at the level of the population of societies.

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